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Dominance network structure across reproductive contexts in the cooperatively breeding cichlid fish *Neolamprologus pulcher*

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Abstract While a large number of studies have described animal social networks, we have a poor understanding of how these networks vary with ecological and social conditions. For example, reproductive periods are an important life-history stage that may involve changes in dominance relationships among individuals, yet no study to date has compared social networks of dominance interactions (i.e. dominance networks) across reproductive contexts. We first analyzed a long-term dataset on captive social groups of the cooperatively breeding cichlid *Neolamprologus pulcher*, and found that eviction events were significantly more common around reproduction than expected by chance. Next, we compared the structure of dominance networks during early parental care and non-reproductive periods, using one of the first applications of exponential random graph models in behavioral biology. Contrary to our predictions, we found that dominance networks showed few changes between early parental care and non-reproductive periods. We found no evidence that dominance interactions became more skewed towards larger individuals, became more frequent between similar-sized individuals, or became more biased towards a particular sex during parental care. However, we did find that there were relatively more dominance interactions between opposite-sex dyads in the early parental care period, which may be a by-product of increased sexual interactions during this time. This is the first study in behavioral ecology to compare social networks using exponential random graph modeling, and demonstrates a powerful analytical framework for future studies in the field [*Current Zoology* 61 (1): 45–54, 2015].

Keywords Social network, Aggression, Submissive, Hierarchy, Parental care, P* model

Dominance is an important type of social relationship that is characterized by consistency in the outcome of agonistic interactions between individuals (Drews, 1993). In many species, dominance is a key contributor to individual variation in resource acquisition, and can therefore influence a diverse array of fitness-linked outcomes, including growth (e.g. Brockmark and Johnsson, 2010), survival (e.g. Arcese and Smith, 1985), predation risk (e.g. Schneider, 1984), parasite exposure (e.g. Courchamp et al., 1998) and access to mating opportunities (e.g. Ellis, 1995). While dominance is fundamentally a relationship between a pair of individuals (Drews, 1993), there is a strong interest in understanding how dominance relationships are structured at the group level. In most cases, animals form orderly (e.g. linear) dominance hierarchies (Shizuka and McDonald 2012), and there are predictable associations between social rank and traits related to size and strength (Francis, 1988; Mesterton-Gibbons and Dugatkin, 1995).

While past studies on dominance hierarchies have revealed important causes and consequences of social rank, there is a dearth of knowledge in understanding patterns of dominance interactions *per se*. In order to explicitly study variation in dominance interactions within social groups, several authors have recommended the use of social network analysis (Shizuka and McDonald, 2012; McDonald and Shizuka, 2012; Pinter-Wollman et al., 2014). In this analytical framework, individuals are represented as nodes, while the dominance interactions that occur among individuals are represented as the edges in the network. Analyzing the structure of these 'dominance networks' provides a complementary approach to the traditional study of dominance hierarchies, in that it allows for tests of complex factors (e.g. indi-

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vidual and dyadic attributes, higher-order processes) that contribute to variation in dominance interactions among dyads, rather than focusing on the association between individual traits and social rank. For example, Dey and Quinn (2014) recently analyzed dominance networks in a cooperatively breeding bird and found that males and females differ in their tendency to use physical aggression and submissive displays, and also that interactions were more frequent among same-sex dyads than among opposite-sexed dyads. One area in which social network analysis may be particularly useful is in understanding how dominance relationships are influenced by social or ecological context (e.g. population density, resource abundance) as these analytical techniques can be used to evaluate changes in the quantity and quality of dominance relationships even when individuals do not change in social rank.

Dominance relationships are expected to change across life-history stages, since the costs and benefits of social status will also vary across theses stages. In many group-living species, reproduction is partially or completely monopolized by socially dominant individuals. As a result, reproductive periods are an important life-history stage in which individuals might challenge others to increase their social rank and access reproductive opportunities. Similarly, dominant individuals may be selected to suppress subordinate reproductive attempts, and such suppression is often done through physical aggression (e.g. Young et al., 2006). In addition, changes in dominance relationships during reproductive periods could be a by-product of the physiological changes that are required for reproduction. For example, many of the hormones that are involved in reproductive physiology have pleiotropic effects, including effects on dominance-related behaviours (Lincoln et al., 1972). While several studies have described differences in aggressive and submissive behaviours during reproduction (e.g. Garrett and Campbell, 1980; Southern and Southern, 1982), no study to our knowledge has evaluated the change in patterns of dominance relationships across reproductive contexts using a social network approach.

In this study, we analyzed patterns of dominance across reproductive contexts, in the cooperatively breeding cichlid *Neolamprologus pulcher*. This fish is endemic to Lake Tanganyika in Eastern Africa, where it forms permanent social groups of 2–20 individuals. Within these social groups, reproduction is highly skewed towards a dominant breeding pair, which is composed of the largest male and female fish (Wong and Balshine, 2011a). Other group members form a size-based queue for the dominant breeding positions, cooperate in raising the group's offspring (Balshine et al., 2001; Heg et al., 2005; Wong and Balshine, 2011a), and may also achieve some reproductive success (Heg and Hamilton, 2008; Heg et al., 2009; Hellmann et al., *in review*). In a previous study, we demonstrated that *N. pulcher* groups have highly orderly dominance networks (i.e. high triangle transitivity; Shizuka and McDonald, 2012) and that interactions within dyads were directionally consistent (Dey et al., 2013). Additionally, we found that dominance interactions were not equally distributed throughout the network, but instead occurred more often among high-ranking individuals (Dey et al., 2013).

To quantify how dominance interactions change with reproductive context, we first analyzed a long-term dataset on captive *N. pulcher* social groups, and tested whether subordinate group members were more likely to be evicted from the group around reproductive events compared to non-reproductive periods. Theory suggests that dominants should evict subordinates who do not contribute sufficiently to the group to offset their residency costs (i.e. 'pay-to-stay', Gaston, 1978), or those subordinates that compete for reproduction with dominant individuals (Johnstone and Cant, 1999). Empirical evidence shows that subordinates in cooperative breeding groups are often evicted as punishment for reproducing, or to prevent reproduction in individuals that are likely to reproduce (e.g. Clutton-Brock et al., 1998, Cant et al., 2010). As a result, evictions are predicted to occur most frequently during reproductive periods, and may represent an extreme endpoint of increases in aggression that arise from increased intra-group conflict during reproduction. A recent study on *N. pulcher* demonstrated that when subordinates were prevented from providing help, they were more likely to receive aggression and be evicted from their group, although this effect was only evident in small groups (Fischer et al., 2014). However, no study on this species has tested whether the timing of evictions is related to reproduction, which if true, would suggest that reproductive conflict is a primary driver of eviction in this species.

In addition to changes in the likelihood of eviction, conflict during reproductive periods could influence changes in dominance networks. To test this hypothesis, we explored how patterns of dominance interactions change between the early parental care period (just after eggs had been laid) and non-reproductive periods. Recent genetic evidence from wild *N. pulcher* suggests that subordinate male and female group members

commonly reproduce (Hellman et al., *in review*). In many species where socially subordinate individuals attempt to gain some parentage, they reproduce just after dominant individuals to avoid detection (and subsequent punishment) or infanticide (e.g. Poikonen et al., 2008; Hodge et al., 2011). Indeed, a study in captive *N. pulcher* social groups showed that when subordinate females reproduce, they also do so shortly after the dominant female in their group has laid (Heg et al., 2009). As a result, conflict over subordinate reproduction during the early parental care period could contribute to changes in the structure of dominance networks. This conflict could be dependent on individual body size and sex, since subordinate reproduction (at least for females) is dependent on body size (Heg et al., 2009), and subordinate reproduction will primarily influence the fitness of same-sex group members. Additionally, changes in dominance network structure during the early parental care period could be due to conflict over the provision of parental and alloparental care. There is evidence that 'lazy' *N. pulcher* receive aggressive punishment from other group members, and increase their helpfulness after enforced idleness (Fischer et al., 2014). Such conflict over cooperative behaviour may be most acute during early parental care periods since eggs require frequent tending to develop. We tested for changes in dominance network structure using exponential random graph models (described below), and specifically focused on how sex and body size differentially influenced the structure of networks during each time period.

1 Materials and Methods

1.1 Methods

1.1.1 Study animals and housing conditions

This study was conducted on laboratory-reared *N. pulcher,* housed at McMaster University, that were descendants of wild caught fish from Lake Tanganyika, Zambia. Each social group was housed in a 189-litre aquarium lined with 3 cm of coral sand substrate that included two inverted terracotta flowerpot halves and six black PVC tubes for use as shelters and spawning sites. Water temperature was maintained at 26 ± 2°C and the housing facility was kept on a 13:11 hour light: dark cycle. All fish were fed commercial cichlid flakes *ad libitum*, six days a week. The methods for animal housing, handling, and study protocols (described below) were assessed and approved by the Animal Research Ethics Board of McMaster University (Animal Utilization Protocol Number 10-11-71) and adhered to the guidelines of the Canadian Council for Animal Care.

1.1.2 Evictions and reproduction

Long-term monitoring data on laboratory social groups were used to test for a temporal correlation between reproductive and eviction events. We considered records over a six year period (January 1, 2007 to December 31, 2012) from 14 aquaria that were continuously occupied. Each aquarium contained a group consisting of a breeder male and female, as well as a variable number of subordinate helpers of each sex. The records for each group included the dates of reproductive events (indicated by eggs in the brood chamber or newly emerged fry) and of eviction events (i.e. a fish being aggressively displaced to the upper part of the aquaria). Fish that were 'evicted' were subsequently removed from the aquaria to avoid further physical aggression. As breeding individuals senesced, and juveniles matured and ascended to breeding positions, the entire social group was occasionally replaced to avoid inbreeding and to ensure that each tank consistently contained both a breeder-sized male and female.

1.1.3 Behavioural observations

To test our predictions related to differential social network structure during the early parental care and non-reproductive periods, we selected 14 social groups for behavioral observations. Social groups selected for this study contained 4 to 8 individuals (mean group size ± *SD* = 5.2 ± 1.2). On August 16, 2013, all fish from these 14 social groups were weighed, measured (standard length), and sexed by examination of their genital papillae. Additionally, each fish was given a unique elastomer tag and/or dorsal fin clip to facilitate individual identification. Neither form of marking had apparent affects on individual behaviour (see also Stiver et al., 2004), and the fish recovered from the procedure immediately. Fish were also assigned a size rank, based on their relative size (in standard length, ties were broken by differences in body mass) within their social group (with rank = 1 indicating the largest individual). In *N. pulcher* groups, dominance rank is highly dependent on body size (Taborsky, 1984, 1985; Wong and Balshine, 2011a).

Three days following fish marking, we began carefully monitoring each group for reproduction by checking possible spawning locations for eggs on a daily basis. After spawning, *N. pulcher* provide intense parental care in the form of brood care (i.e. aerating eggs, micronipping) and defense, while the eggs and larvae are still attached to the breeding substrate (0–7 days after spawning; Taborsky, 1984). When eggs were first detected in each group, we performed a behavioral obser-

vation (see below for details) on that group the following day. A second behavioral observation was performed 24 hours after the first observation, such that for each social group we performed two behavioral observations during the early parental care period (i.e. 0–3 days after spawning, and always during the egg stage). We performed two additional behavioral observations during the non-reproductive period. These occurred on the 14th and 15th day following the first behavioral observation (i.e. 14–17 days after spawning). At this stage, the young are free swimming, have absorbed their yolk sac and are obtaining their own food independently. While adult *N. pulcher* will defend their territory year-round (and indirectly defend any young in the territory), there is no direct parental care occurring at this stage.

All behavioral observations were conducted between 13: 00 and 16: 00 h by the same observer (Q.Y.J.T.). The observer sat approximately 1.5 m from the focal aquarium, and allowed the fish to acclimate for 5 minutes prior to the start of each observation period. The observer then recorded all dominance-related interactions that occurred among group members for 15 minutes. These behaviours were grouped into two main categories: aggressive interactions (i.e. aggressive posture, frontal display, chase, ram, bite, mouth fights) and submissive interactions (submissive posture, submissive display, displacement, flee), based on a recent ethogram for this species (Sopinka et al., 2009; Hick et al., 2014). For each interaction, the observer also recorded the identification of both the actor and the receiver.

1.2 Statistical analysis

All analyses were performed in the R statistical package, version 3.0.1 (R Core Team 2013). We used a permutation approach to test for a temporal correlation between reproductive events and eviction events. For each eviction event in each aquarium (n = 582 events), we determined the number of days to the nearest reproductive event (n = 394) in that aquarium. We then summed these difference values across all eviction events in all aquaria, to generate an observed test statistic representing the total difference in time between eviction and the nearest reproductive event. We compared this test statistic to similar values generated in 1,000 permuted data sets. For each permutation, we randomized when the eviction events occurred in each aquarium by randomly sampling the dates in the study period (i.e. January 1, 2007 to December 31, 2012) without replacement, and conserving the number of evictions that occurred in each aquarium. Then, we calculated the total difference in the time between these randomized eviction events and the nearest reproductive events, for each permuted dataset. The distribution of values generated from the 1,000 permutations was compared to the observed test statistic, to generate a one-tailed P-value related to whether the observed eviction events were more likely to occur near reproductive events than expected by random. It is possible that our data set is biased towards under recording reproductive events, which are more difficult to observe than evictions and occasionally go undetected within our laboratory (e.g. if eggs are laid in a an atypical spot and are not detected). However, because our analysis considers the closest reproductive event to each eviction event, any missing reproductive events should increase the test statistic and therefore make our analysis more conservative.

Our analysis of dominance network structure was conducted using the *statnet* (Handcock et al., 2008; Handcock et al., 2014a), *ergm* (Hunter et al., 2008; Handcock et al., 2014b) and *ergm.count* (Krivitsky, 2013) packages in R (R Core Team, 2013). For each social group, we built a weighted dominance network for the early parental care period and for the non-reproductive period. Given that this study represents an exploratory analysis of how network structure varies across reproductive contexts, and that directional networks based on aggressive interactions were highly correlated with transposed networks based on submissive interactions (i.e. the actor and receiver were flipped) (Mantel test: 5000 permutations, r_s = 0.34, P = 0.0004 and r_s = 0.43, P = 0.0002 for the early parental care and non-reproductive period respectively), we chose to combine all aggressive and submissive interactions into a single, undirected dominance network for each time period. While analyzing directed networks could have allowed us to test more specific hypotheses, this study focused on broad-scale changes in social conflict between time periods. Therefore, we analyzed undirected networks similar to those previously used to explore social conflict in this species (Dey et al., 2013). The weight of the edges in these networks was the total number of dominance interactions that occurred between the dyad, pooled across the two behavioral observations for each time period. Separate networks generated for each of the two observation periods within each time period were highly correlated (Mantel test: 5000 permutations, r_s = 0.79, P = 0.0002 and r_s = 0.85, P = 0.0002 for the early parental care and non-reproductive period respectively), suggesting that the networks

were stable across observations and that our sampling period provided a robust estimate of true network structure. In one social group a 'budding' event occurred, where a subordinate female established a distinct territory within the aquarium and laid her own clutch 1 week after the dominant breeding female had laid (see also Limberger, 1983). This group was excluded from all analyses, and thus the resultant analyses were conducted on the remaining 13 social groups.

We analyzed network structure using exponential random graph models (ERGMs) (Wasserman and Pattison, 1996; Snijders et al., 2006). Similar to logistic regression, these models predict the presence (or weight) of edges based on various independent variables. Because ERGMs can simultaneously consider multiple independent variables, they allow for powerful tests of the factors that contribute to network structure. For this reason they have been widely used in the study of human social networks (Lusher et al., 2012), although their application to non-human animal networks has been restricted to only three previous studies that we are aware of (Ilany et al., 2013; Dey and Quinn, 2014; Edelman and McDonald, 2014). As a first step in exploring the changes in network structure between early parental care and non-reproductive periods, we created separate models for each of these time periods. In each model, we used a supernetwork composed of all 13 social groups as the observed (i.e. response) network and restricted the edges in our models to only occur within groups to retain this structure. We considered 5 independent variables in each model: (1) the 'sum' term, which is similar to an intercept in linear modeling, (2) individual effect of sex, which tests whether males or females are more likely to be involved in dominance interactions, (3) individual effect of size rank, which tests whether an individual's relative size influences their likelihood to be involved in dominance interactions, (4) sexual homophily, which tests whether there is an increased likelihood of interactions between same-sex dyads and (5) dyadic effect of the difference in log (standard length), which tests whether interactions are more likely to occur among dyads that have similar body size.

In addition to considering separate models of the early parental care and non-reproductive periods (above), we also examined the factors that contribute to changes in network structure by performing a similar analysis on a 'difference network'. This difference network was composed of the same set of nodes as the supernetworks above, but each edge weight was the difference in the number of interactions between the early parental care and non-reproductive periods. To create a graph where all edge weights were non-negative numbers, we then added the absolute value of the minimum edge weight (i.e. -29) to all within-group edge weights. The resulting graph ranged in edge weight from 0 to 59, where low edge weights were indicative of fewer interactions during the early parental care period (relative to the non-reproductive period), and high edge weights were indicative of more interactions during the early parental care period. Again, the model restricted ties to only occur within groups, and was fitted with the same 5 independent terms described above. In this case however, the model estimates indicated the effect that each variable had on the change in dominance interactions between the two time periods. All three models were fitted according to the recommendations in Goodreau et al. (2009), Krivitsky (2012) and Lusher et al. (2012). Models required the use of a Markov-chain Monte Carlo (MCMC) estimation technique to approximate the maximum likelihood (Lusher et al., 2012) and we specified a chain length of ten million, a sampling interval of five thousand and a burn-in of fifty thousand proposals. We used Poisson reference graphs for each model. The difference network is based on differences in counts, which are known to be Skellam distributed (Skellam, 1946). However Skellam reference graphs are not implemented in *ergm. count* and the Poisson model fit the data well. Additionally, adjusting the reference graph to a Conway-Maxwell-Poisson distribution did not improve the model fit (Krivitsky, 2012). Visual analysis of MCMC sample statistics, as well as networks simulated from the fitted models, did not show any evidence of degeneracy. Additionally, models were checked for goodness of fit by examining the distributions of nodal strength (i.e. weighted degree) from 100 simulated networks from each model, and comparing those distributions to the observed networks (see also Goodreau et al., 2009).

2 Results

Eviction events in *N. pulcher* social groups were significantly more likely to occur near reproduction than expected by chance (permutation test: mean difference in days between evictions and nearest reproductive event = 40.2, mean difference in permuted data sets = 45.8, $P = 0.003$, Fig. 1). Evictions were most likely to occur 1 day prior to when reproduction was recorded (i.e. media*n* = -1), although there was a large degree of variation (Fig. 1: 25th percentile = -27 days, 75th percentile = +18 days).

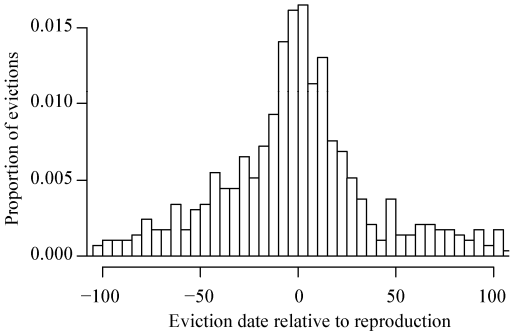

Fig. 1 Histogram of the date of eviction events (n = 582 events) relative to the nearest reproductive event pooled across 14 *N. pulcher* social groups

Evictions were more likely to occur near reproductive events than expected by chance (see text for details).

Separate ERGMs on the early parental care and non-reproductive periods networks showed similar estimates for all independent variables (Table 1, Fig. 2). Both models showed that dominance interactions were more likely to involve high-ranking individuals (negative effect of rank: Table 1) and were more likely to occur among dyads with a small difference in body size (negative effect of size difference: Table 1). Neither model demonstrated a difference in dominance interactions depending on individual sex (non-significant effect of sex: Table 1), however there was an increased likelihood for dominance interactions to occur among opposite-sex dyads relative to same-sex dyads (negative effect of sexual homophily: Table 1).

The difference network (Fig. 3) demonstrated limited changes in network structure between early parental care and non-reproductive periods. We found no significant effect of sex, rank or size difference on the change in dominance interactions (Table 2). We did find a significant, negative effect of sexual homophily in this network (Table 2; effect of homophily), suggesting that dominance interactions became less sexually homophilic during the early parental care period.

3 Discussion

Patterns of behavioral interactions among members of a social group can be influenced by a variety of social and ecological factors. In this study, we explored how patterns of dominance interactions vary with reproductive context in a highly social, cooperatively breeding fish. We found that aggressive eviction events are more likely to occur near reproduction than expected by chance, suggesting that reproductive conflict is an important contributor to eviction in this species. However, the structure of dominance networks showed relatively little change between the early parental care and non-reproductive periods. Dominance interactions did not become more concentrated among individuals of large or small body size, nor did they differ according to the size difference among individuals. Additionally, there was no change in the relative frequency of dominance interactions involving each sex. We did observe a significant decrease in sexual homophily (i.e. relatively more interactions between opposite-sexed dyads) during the early parental care period, however this finding was opposite our prediction of increased reproductive conflict during this life-history stage. Taken together, these results suggest that dominance networks in *N. pulcher* may be relatively stable across reproductive contexts.

In a previous study (Dey et al., 2013), we also analyzed the structure of dominance networks in this species. Consistent with the current study, and with studies on social insects (Chandrashekara and Gadagkar, 1992; Monnin and Peeters, 1999; Cant et al., 2006), our previous study also found that dominance interactions were more likely to occur among high-ranking individuals (Dey et al., 2013). In high reproductive skew societies (such as *N. pulcher*) the value of social position rises exponentially with increasing rank. As a result, the cost of changing rank is higher for higher-ranked individuals,

Table 1 Exponential random graph model results for *N. pulcher* dominance networks during reproductive and non-reproductive periods

Model term	Reproductive period			Non-reproductive period		
	Estimate	*SE*	*P* - value	Estimate	*SE*	*P* - value
Sum	3.29	0.10	< 0.0001	3.42	0.10	< 0.0001
Sex [male]	-0.006	0.06	0.92	0.02	0.05	0.64
Rank	-0.15	0.01	< 0.0001	-0.19	0.01	< 0.0001
Sexual homophily	-0.48	0.07	< 0.0001	-0.17	0.06	0.006
Size difference	-0.60	0.16	0.0001	-0.46	0.15	0.002

Significant *P*-values are shown in italics.

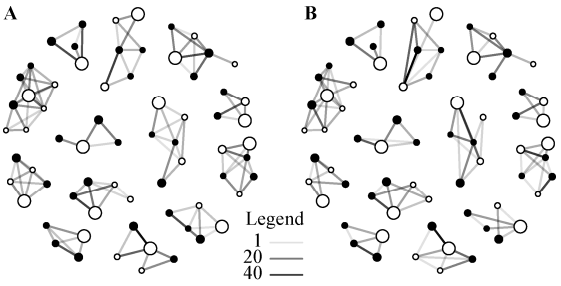

Fig. 2 Dominance network structure of *N. pulcher* social groups during early parental care (A) and non-reproductive periods (B)

Node orientation was determined using the Fruchterman-Reingold algorithm and shows individuals clustering in 13 social groups. Node size was scaled to social rank (with largest nodes indicating highest ranking individuals), while node colour indicates sex (black = female, white = male). Edge colour indicates the number of dominance interactions that occurred between each dyad, with darker lines indicating more interactions (see legend).

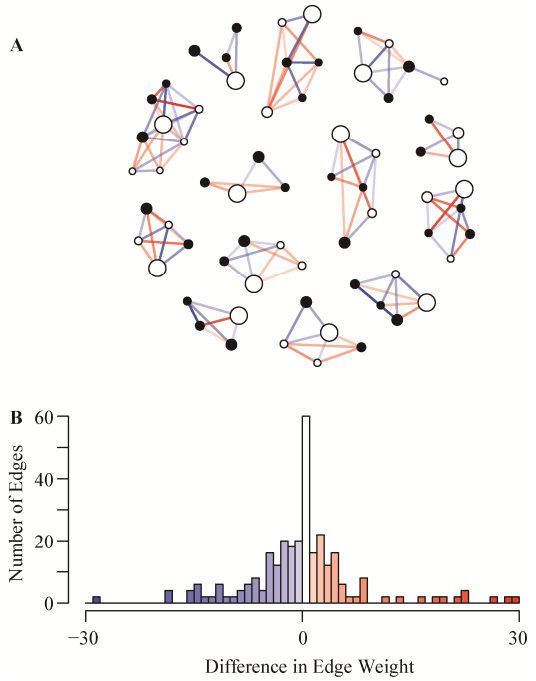

Fig. 3 (A) Social network of the difference in dominance interactions between early parental care and non-reproductive periods. Edge colour (red = more interactions during early parental care, blue = more interactions during the non-reproductive period) and darkness (darker lines = greater disparity between reproductive and non-reproductive period) indicate the differences in number of interactions. Node orientation is identical to that in Fig. 2. (B) Density histogram of edge weight from this network, excluding structural zeros (i.e. inter-group edge weights). Bar colour matches the edge colour from panel A.

Table 2 Exponential random graph model results for the change in dominance interactions between reproductive and non-reproductive periods

Model term	Estimate	*SE*	*P*-value
Sum	3.32	0.05	< 0.0001
Sex [male]	-0.01	0.02	0.64
Rank	0.01	0.006	0.10
Sexual homophily	-0.07	0.03	0.03
Size difference	-0.002	0.07	0.97

Positive estimates indicate an increase in the influence of the variable during the reproductive period, relative to the non-reproductive period. Significant *P*-values are shown in italics.

and establishing dominance relationships may be more important for these individuals (see also Wong and Balshine, 2011b).

The current study, which used a new statistical technique (as well as new behavioral data), revealed additional structure in *N. pulcher* dominance networks that was not observed in our previous study. We found that dominance interactions are more likely to occur among similar-sized individuals, even after controlling for each individual's size rank. This finding is consistent with theoretical predictions about conflict in size-structured groups, since relative fighting ability may be uncertain in similar-sized dyads (Enquist and Leimar, 1983), and because subordinates should challenge dominants more frequently if the difference in fighting ability is small (Cant and Johnstone, 2000). Indeed, Reddon et al. (2011) found that staged contests between *N. pulcher* were almost always won by the larger fish if the size asymmetry was greater than 5%, but when contestants had a size asymmetry of less than 5% contest outcome was not predicted by relative size. A previous experimental study on *N. pulcher* also showed that a small size difference between the breeder male and the largest male helper led to increased conflict, although this conflict was displayed as increased submissive displays rather than increased aggression (Hamilton et al., 2005, see also Heg et al., 2004). Interestingly, there is good evidence that relative size does not have a strong influence on conflict among females (Hamilton and Heg, 2008; Heg, 2010), and so there may be a complex interaction between sex and relative size on patterns of dominance interactions.

In addition to a strong effect of relative size, we also found that dominance interactions were more likely to occur among opposite-sexed pairs. This finding was opposite our predictions, since only same-sex individuals need to compete for breeding positions. However,

frequent intersexual dominance interactions during the early parental care period may be a by-product of intersexual interactions in general (e.g. for courtship and reproduction). This does not explain why intersexual dominance interactions are also relatively common during non-reproductive periods, and further study will be needed to understand this phenomenon.

Although we found that eviction events were more likely to occur close to spawning events, our network analysis did not reveal major changes in dominance networks between the early parental care and non-reproductive periods. It may be the case that changes in dominance interactions during reproduction only occur in certain situations (e.g. in unstable groups where dominance hierarchies are not fully established), but that these changes are manifested in a dramatic increase in aggression and eviction. In stable social groups (including all 13 groups considered in this study) there may be few changes in dominance network structure across reproductive contexts, especially if subordinates do not directly compete for dominant breeding positions and if subordinate reproduction does not significantly decrease the reproductive success of dominants. Additionally, the apparent discrepancy between eviction rates and dominance network structure in our study might be the result of the timing of our behavioral observations. Dominance interactions may show the largest changes just prior to reproduction when changes in dominance rank could lead to changes in reproductive success. This idea is consistent with our findings from our long-term data set, which suggest that eviction events are most likely to occur 1 day prior to reproduction. Unfortunately, there are no obvious reliable cues of impending reproduction in *N. pulcher* that would have allowed us to perform our observations prior to spawning. It is possible that dominance networks may have quickly returned to non-reproductive baselines after spawning and that we may have missed a transient change in dominance networks structure due to our observation timing. As a result, future studies that are able to observe *N. pulcher* dominance interactions just prior to reproduction would be highly valuable, although they may be difficult to conduct.

There may also be differences in dominance networks between wild and captive *N. pulcher* that could influence the findings in this study. Although our captive groups simulated the natural composition and territory size of wild *N. pulcher* groups (Balshine et al., 2001), the captive environment lacks much of the complexity found in nature. In particular, captive subordinate *N. pulcher* do not have any option to disperse to another group to breed, and such outside options are key theoretical factors that influence aggressive interactions among members of social groups (Cant and Johnstone, 2009; Nonacs and Hager, 2011). It may be the case that captive *N. pulcher* are more reluctant to challenge dominants for breeding positions during reproductive periods, because they cannot leave the group if they fail to usurp. Alternatively, captive subordinates may be more likely to challenge dominants within their group because it is their only chance to achieve breeding status. Since it is difficult to predict which aspects of network structure are influenced by the captive environment, empirical studies that directly compare social networks between captive and wild *N. pulcher* would be extremely valuable.

By performing behavioral observations on replicate social groups we provide a robust comparison of dominance network structure during two life-history stages in a well studied cooperatively breeding fish species. Our study revealed novel factors influencing dominance network structure in *N. pulcher*, and suggests that dominance networks are relatively stable across reproductive contexts, at least in captive social groups. We also demonstrate the utility of exponential random graph models for testing multivariate hypotheses in behavioral ecology. This analytical technique that has been used in only a small number of studies on animal social networks, but has widespread applicability in this field and will likely increase in popularity in the future.

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